

## ALGAL PIGMENTS, MEIOFAUNA, AND MACROFAUNA FROM TWO EDAPHIC SALT MARSH MICROHABITATS IN GALVESTON BAY, TEXAS, USA

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**Abstract:** Small-scale spatial patterns in abundance on the salt marsh surface were examined by comparing microalgal pigment concentrations and densities of meiofauna and macrofauna between interculm and interplant microhabitats in low-elevation edge natural and created marshes of Galveston Bay, Texas, USA. The interculm microhabitat consisted of sediments located within clusters of *Spartina alterniflora* culms, and the interplant microhabitat was located between clusters of culms. Paired interculm and interplant sediment samples were taken from 16 marshes in both fall and spring. No significant differences were found in concentrations of chlorophyll *a* or pheophytin *a* between microhabitats. The biomass of macroorganic matter was significantly greater in the interculm microhabitat. The meiofauna was dominated by nematodes and the macrofauna by annelid worms and peracarid crustaceans. Mean densities of almost all meiofaunal and macrofaunal taxa were greater in interculm samples, although not all differences were statistically significant. No taxa had significantly greater densities in interplant samples. Although sampling techniques can affect results, these data agree with small-scale distributional data from other low-elevation, salt marsh habitats. The interculm microhabitat should be considered when sampling organisms in salt marshes, as well as the more typically sampled interplant microhabitat. The interculm microhabitat at Galveston occupied between 9.5 and 31.9% of the marsh surface.

**Key Words:** salt marsh, *Spartina alterniflora*, benthic microalgae, meiofauna, macrofauna, macroorganic matter

### INTRODUCTION

Salt marshes in the northern Gulf of Mexico provide food and shelter for many adult and juvenile organisms of ecological, commercial, and recreational importance (Boesch and Turner 1984). These marshes are often dominated by smooth cordgrass, *Spartina alterniflora* Loisel., and comparisons between the vegetated marsh surface and adjacent, nonvegetated surface have documented differences in assemblages of microalgae (Maples 1982, Blanchard and Montagna 1992), meiofauna (Fleeger 1985, Sun et al. 1993) macroinfauna (Zimmerman et al. 1991, Minello and Webb 1997, Whaley 1997),

and nekton (Zimmerman and Minello 1984, Minello 1999, Rozas and Zimmerman 2000). However, the vegetated areas of a salt marsh are not homogeneous, and the abundance of organisms within this habitat is affected by small-scale patterns on the marsh surface. For example, microtopography and the presence of pools and depressions alter abundance patterns of meiofauna and small nekton (Kneib 1984a, Sun et al. 1993, Sun and Fleeger 1994), and elevation and distance from the marsh-water interface affect populations of algal epiphytes (Jones 1980), meiofauna (Teal and Wieser 1966, Coull et al. 1979), macrofauna (Rader 1984, Kneib 1984b, 1992, Covi and Kneib 1995, Whaley 1997), and nekton

(Baltz *et al.* 1993, Minello *et al.* 1994, Peterson and Turner 1994, Minello 1999, Rozas and Zimmerman 2000).

The marsh plants themselves can also affect the small-scale distribution and abundance of organisms. Epiphytic communities that exist on the plant surfaces differ from those found on the sediment surface (Day *et al.* 1973, Wu 1994), and Rutledge and Fleeger (1993) documented greater densities of meiofauna on *Spartina alterniflora* stems than on marsh sediments during some months. Within sediments, however, spatial relationships between the marsh plants and distributions of microalgae or animals have not been extensively studied. In a South Carolina high-elevation marsh (tidally inundated about 6–8 h per day), Bell *et al.* (1978) reported no differences in meiofaunal density from sediments within a 1.5-cm radius of *S. alterniflora* culms when compared with samples from sediments “between” (i.e., remote from) culm clusters, and they also found no positive relationship between meiofauna density and root biomass. In a nearby low-elevation marsh, however, Osenga and Coull (1983) reported a positive relationship between the abundance of nematodes and the density of live *S. alterniflora* roots. In North Carolina, Rader (1984) found that macroinfaunal and meiofaunal densities were greater in samples containing *S. alterniflora* culms than in samples from “bare sediment.” The difference in macrofaunal densities decreased with increasing marsh surface elevation (and decreasing inundation periods). Salt marsh inundation patterns in the northern Gulf of Mexico are quite different from those on the Atlantic coast of the U.S. (Rozas and Reed 1993, Rozas 1995), and the marsh edge habitat in Galveston Bay, Texas is almost constantly flooded during spring and fall (Minello and Webb 1997). Spatial patterns of organisms in relation to *S. alterniflora* culms, therefore, may be different in this low elevation and frequently inundated salt marsh habitat. Goldberg (1996) found that macrofaunal densities (mainly peracarid crustaceans) in Galveston Bay were greater in sediment cores that contained *S. alterniflora* stems (i.e. culms) than in cores without stems.

In the present study, abundances of edaphic microalgae, meiofauna, and macrofauna within Galveston Bay marshes were examined in relation to *S. alterniflora* culms on the vegetated salt marsh surface in fall and spring. Sediments within clusters of culms were termed the interculm microhabitat and were compared with sediments from bare areas between clusters of culms, termed the interplant microhabitat. The null hypotheses that the following parameters did not differ between the two salt marsh microhabitats was tested: 1) concentration of chlorophyll *a* and pheophytin *a*, 2)

biomass of macroorganic matter, and 3) density and taxonomic composition of meiofauna and macrofauna.

## METHODS

### Location and Timing of Sampling

Paired interculm and interplant sediment samples were in taken in September 1990 and May 1991 from a total of 16 *Spartina alterniflora* salt marshes in Galveston Bay (Figure 1). The alongshore location of a sample pair was determined by randomly selecting distances from fixed shoreline locations in each marsh. All samples were obtained from vegetated sediments near the marsh edge (approximately 1 m from the marsh-water interface). The clusters of culms in the marshes studied were roughly circular in shape and contained from a few to 50 or more culms each, averaging about 30. The average height of the culms varied from marsh to marsh, ranging from 0.3 to 0.7m. Additional information on the physical characteristics and animal-use patterns in these marshes can be found in Delaney (1994), Minello and Webb (1997) and Delaney *et al.* (2000).

Interculm and interplant samples were collected in conjunction with a larger project comparing natural and created salt marshes. In September 1990, 15 marshes (five natural marshes (N1–N5) and 10 created marshes (T1–T10)) were sampled. By May 1991, the T7 marsh had been covered with dredged sediment and was replaced in the sampling design with a previously unsampled natural marsh (designated N6). Results comparing natural and created marshes have already been reported for the interplant macrofauna samples (Minello and Webb 1997), and meiofauna and microalgae comparisons will be reported elsewhere. Although differences between natural and created marshes exist for some of these parameters, initial analyses showed that there were no significant interactions between interculm-interplant relationships and whether the marshes were natural or created. Therefore, no distinction was made between natural and created marshes in the data analysis for this report. Paired t-tests were used to compare corresponding interculm and interplant samples for all parameters examined;  $N = 45$  for algal pigment and meiofauna samples and  $N = 30$  for macroorganic matter and macrofauna samples for each season and microhabitat.

### Algal Pigments and Meiofauna

Twelve sediment samples (six pair) were taken from each of the 15 marshes during two seasons (total samples = 360, 180 per season). One member of each sample pair was taken from the approximate center of

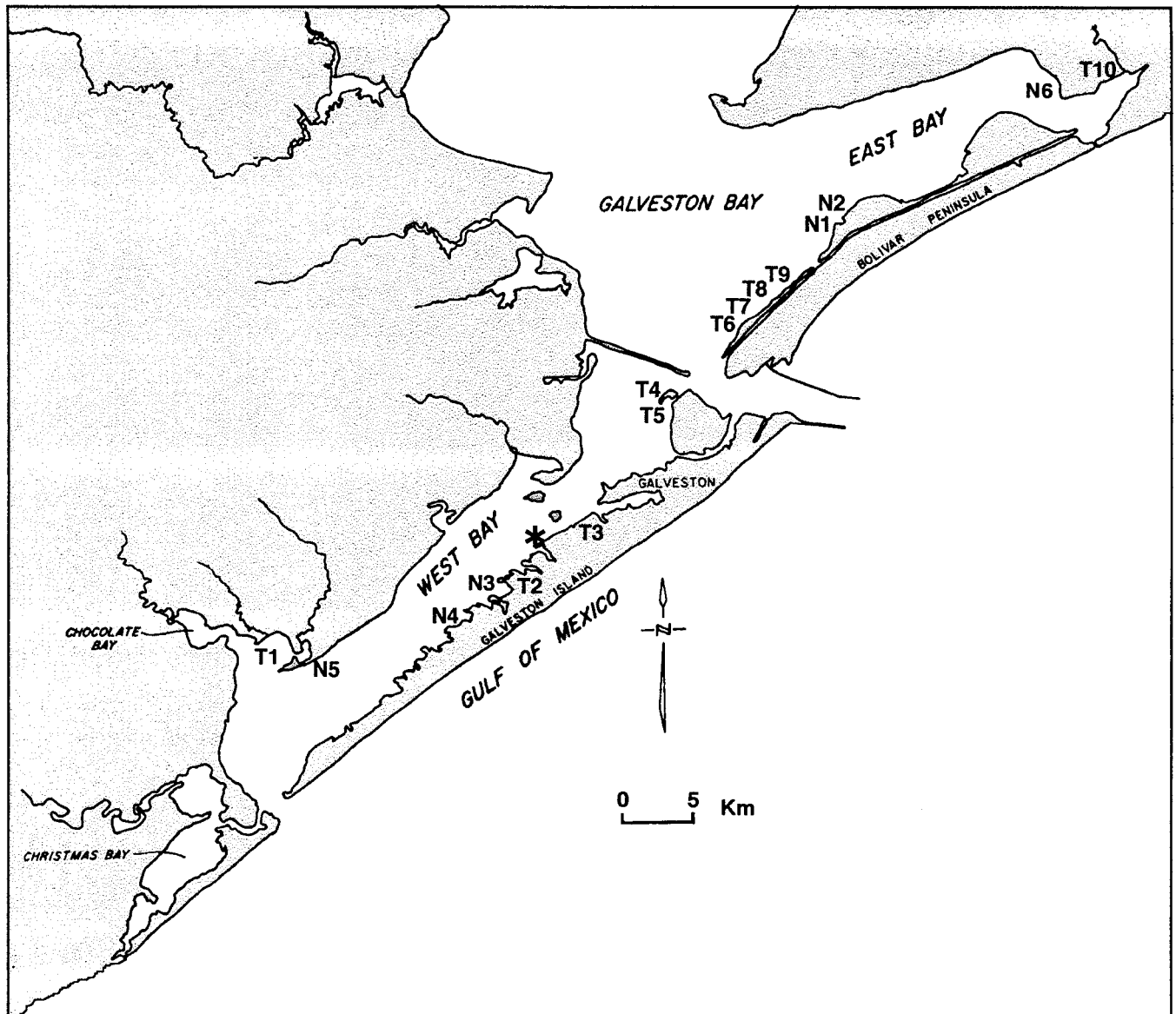


Figure 1. Location of 16 *Spartina alterniflora* salt marshes sampled in lower Galveston Bay, Texas. Aerial coverage of interculm and interplant microhabitats was estimated from the marsh location indicated by the asterisk. N = natural marshes; T = created (transplanted) marshes.

the interculm sediment. The other was taken from the adjacent interplant sediments at a point approximately equidistant (10–25 cm) from the three or four nearest surrounding plants (i.e., clusters of culms, Figure 2).

Samples were obtained with a coring tube of 2.2 cm internal diameter and a surface area of 3.8 cm<sup>2</sup>. Cores were sealed and kept on ice during transport. Cores intended for pigment analysis were wrapped in aluminum foil to prevent exposure to light. In the laboratory, sediments were partially extruded and trimmed to a final sediment depth of 5 cm prior to processing (this depth was selected for consistency with meiofauna and macrofauna samples). Sediments from three pairs of cores from each marsh each season (180 total

cores, 90 per season) were analyzed for chlorophyll *a* and pheophytin *a* concentration. The method involved spectrophotometric acidification and partitioning of acetone with hexane (Whitney and Darley 1979) and was used to correct for the presence of sediment-associated chlorophyll *a* degradation products (chlorophyllide *a* and phaeophorbide *a* in acetone phase and chlorophyll *a* and phaeophytin *a* in hexane phase).

Sediments from the three remaining pairs of sediment cores from each marsh and season were analyzed for meiofaunal abundance and community composition based on major taxa. Sediments were rinsed successively through a 500- and a 63- $\mu$ m sieve. The material retained on the smaller sieve was preserved in a

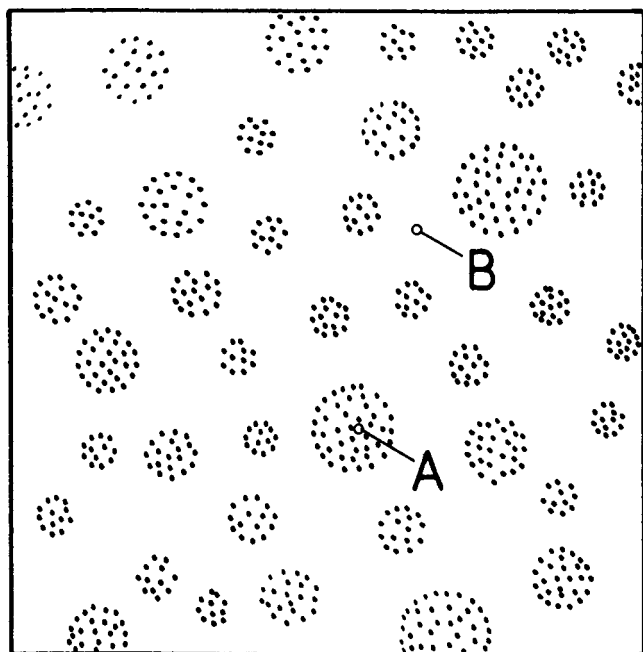


Figure 2. Diagrammatic representation of the surface of 1 m<sup>2</sup> of a typical Galveston Bay *Spartina alterniflora* salt marsh showing the placement of algal pigment and sediment cores for interculm (A) and interplant (B) samples. Each dot represents the point of emergence of a single culm from the sediment surface.

10% formalin solution with rose Bengal. Prior to analysis, the sieved material from each sample was divided into eight aliquots with a Jensen (1982) sample-splitting device, modified as recommended by Pfannkuche and Thiel (1988). Successive one-eighth aliquots of the sieved material from each sample were analyzed in their entirety until at least 500 animals were recorded and identified to major taxa at magnifications of 10X to 400X.

#### Macrofauna and Macroorganic Matter

Paired sediment samples (interculm and interplant) for macrofauna and macroorganic matter were obtained with a 10-cm internal diameter (78.5 cm<sup>2</sup>) corer. Two pair of cores were obtained from each marsh during each season as described above for algal pigments and meiofauna. The interculm member of each core pair included a living *Spartina alterniflora* plant (cluster of culms). The interplant member of the pair was taken from sediments between plants and did not include any living culms. Sediments were extruded and trimmed to a depth of 5 cm, and when present, culms were trimmed to a height of 5 cm. Samples were rinsed onto a 0.5-mm-mesh sieve, and all material retained was preserved in 10% formalin with rose Bengal stain.

In the laboratory, animals were separated from pre-

served plant material and detritus, but organisms that had burrowed into *Spartina alterniflora* stems were not recovered. Polychaete annelids and peracarid crustaceans were identified to the species level when possible, while oligochaetes and other animals were identified at higher taxonomic levels. For measurements of macroorganic matter (MOM), the above-ground portions of *S. alterniflora* culms were removed from samples and discarded. The remaining below-ground biomass of roots, rhizomes, and detritus was then dried at 100 C to a constant weight.

#### Aerial Coverage of Microhabitats

The relative area of different microhabitats within a *Spartina alterniflora* marsh was measured at a natural marsh on Galveston Island located several km northeast of the N3 marsh (Figure 1). A 0.25-m<sup>2</sup> square frame was used to collect six randomly located samples of the marsh surface between 1 and 3 m from the marsh-water interface. Within each quadrat, we measured the number of plant clusters, the circumference of each cluster, the number of culms in each cluster, and the diameter of each culm at the sediment surface. The total horizontal surface area occupied by each cluster and by the culms in each cluster was calculated (by summing the cross-sectional areas of all culms in the cluster). From these data, the area of sediment surface within plant clusters (interculm microhabitat) and between clusters (interplant microhabitat) was estimated.

## RESULTS

Microscopic examination revealed that pennate diatoms were the dominant microalgal component in all samples in both microhabitats during each season. Dominant genera included *Navicula*, *Nitzschia*, *Amphora*, *Achnanthes*, and *Denticula*. Filamentous blue-green algae (cyanobacteria), chlorophytes, and unicellular flagellates (euglenophytes, dinophytes, haptophytes, and cryptophytes) were relatively minor floral components. Chlorophyll *a* and pheophytin *a* concentrations did not differ significantly between interculm and interplant microhabitats (Table 1). In contrast, biomass of macroorganic matter was nearly twice as large in interculm as in interplant samples (1.89x in fall and by 1.70x in spring). These differences were highly significant (Table 1).

Meiofaunal samples were dominated by Nematoda in all marshes in both seasons. Nine major meiofaunal taxa were observed in fall and 10 in spring (Table 1). Mean meiofaunal population densities (all taxa combined) were greater in the interculm microhabitat in both seasons, but the differences were not statistically



Table 1. Concentration of algal pigments ( $\mu\text{g}/\text{cm}^{-3}$ ), biomass of macroorganic matter ( $\text{g}/\text{m}^{-2}$ ), and density of meiofauna (no.  $0.01 \text{ m}^{-2}$ ) from interculm and interplant sediments in lower Galveston Bay salt marshes in fall 1990 and spring 1991. Mean values and standard errors (SE) are shown. P values are from paired t-tests;  $n = 45$  pair for pigments and meiofauna, and  $n = 30$  pair for macroorganic matter.

Parameter	Fall 1990					Spring 1991				
	Interculm		Interplant		P	Interculm		Interplant		P
	Mean	(SE)	Mean	(SE)		Mean	(SE)	Mean	(SE)	
Chlorophyll <i>a</i>	0.68	0.090	0.78	0.120	0.231	0.99	0.125	0.94	0.100	0.708
Pheophytin <i>a</i>	0.14	0.048	0.16	0.044	0.441	0.13	0.044	0.11	0.028	0.449
MOM	996.3	153.4	526.2	98.0	0.001	1052	152.2	620.6	123.1	0.013
Total Meiofauna	3478.1	381.5	2918	359.1	0.077	2819	215.7	2403.0	255.6	0.093
Turbellaria	31.8	4.0	27.0	4.1	0.179	65.4	12.7	42.9	6.6	0.062
Nematoda	2828.7	344.1	2431	315.1	0.167	2369	201.7	2095.8	243.9	0.248
Kinorhyncha	22.2	8.3	35.8	14.5	0.208	14.2	7.9	13.8	6.1	0.961
Tardigrada	0.0	0.0	0.0	0.0		14.0	6.9	10.9	4.0	0.567
Crustacean Nauplii	197.4	42.4	131.5	21.9	0.092	80.8	14.6	62.4	16.1	0.239
Copepoda	247.2	49.7	163.4	31.4	0.037	185.5	27.1	91.1	18.2	0.001
Ostracoda	56.5	11.1	35.1	6.8	0.053	26.7	6.4	29.7	8.0	0.613
Acarina	7.6	1.3	6.5	1.8	0.632	5.1	1.4	5.8	2.0	0.703
Annelida	95.8	16.7	61.6	10.0	0.021	52.3	6.0	39.8	5.8	0.039
Mollusca	12.4	4.7	10.9	2.8	0.071	3.0	1.1	1.9	1.2	0.247

significant. Densities of most individual taxa were also greater in the interculm microhabitat. In fall and spring these differences were statistically significant for Copepoda and Annelida (Table 1.)

The macrofaunal assemblage was dominated by annelid worms and peracarid crustaceans (Table 2). Mean macrofaunal densities for all taxa combined were significantly greater in the interculm microhabitat in both fall and spring, but this difference was barely significant ( $p = 0.044$ ) in fall. The annelids were dominated by polychaetes, and the surface deposit feeder *Streblospio benedicti* Webster, 1879 was the most abundant species identified. The overall densities of both polychaetes and oligochaetes were significantly greater in the interculm microhabitat in spring but not fall. Mean densities of most species identified were greater in the interculm microhabitat, but few of these differences were statistically significant. Peracarid crustacean assemblages were dominated primarily by amphipods; population densities of which were significantly greater in the interculm in spring. The tanaid *Hargeria rapax* (Harger, 1879) was also relatively abundant, and densities were significantly greater in the interculm microhabitat in fall but not in spring.

Measurements on the marsh surface indicated that the aerial coverage of these two microhabitats is quite variable. For example, the percentage of interculm sediments (i.e., area of sediments within a cluster of culms) ranged from 9.5 to 31.9% for the six quadrats examined. From overall mean values, it was estimated that 2.3% (SE = 0.33) of the area was covered by culms, 18.6% (SE = 3.52) of the area was interculm

sediment, and 79.1% (SE = 3.84) of the area was interplant sediment.

## DISCUSSION

Chlorophyll *a* data revealed no significant differences in algal standing crop biomass between the interculm and interplant microhabitats in either season. Because pheophytin *a* concentrations are indicative of the level of metazoan herbivory (Bianchi et al. 1988), the data also suggest that herbivory did not differ significantly between the two microhabitats. Fleeger et al. (1999) suggested that a common herbivore in these marshes, the daggerblade grass shrimp *Palaeomonetes pugio* Holthius, 1949 is not an efficient grazer on edaphic microalgae but has high grazing rates on epiphytic algae located on *S. alterniflora* stems.

Mean densities of total meiofauna were greater in the interculm sediments in the spring and fall (Table 1), but the differences were not statistically significant at the 5% level. Densities of meiofaunal annelids and copepods were significantly greater in interculm sediments during both seasons. Overall macrofaunal densities were also significantly greater in the interculm microhabitat (Table 2). Annelids dominated the macrofauna, and in spring, densities of both polychaete and oligochaete annelids were significantly greater in the interculm microhabitat, as were densities of amphipods. Mean densities of almost all meiofauna and macrofauna were higher in interculm samples, and no taxa had significantly greater densities in interplant samples. These density patterns are generally similar

Table 2. Mean macrofauna population densities (no. 0.1m<sup>-2</sup>) and standard errors (SE) from interculm and interplant samples in lower Galveston Bay salt marshes in fall 1990 and spring 1991. P values are from paired t-tests; n = 30 pairs.

Taxon	Fall 1990				Spring 1991					
	Interculm		Interplant		P	Interculm		Interplant		
	Mean	(SE)	Mean	(SE)		Mean	(SE)	Mean	(SE)	
ALL TAXA COMBINED	1195.0	332.5	516.4	133.8	0.044	910.9	142.7	523.6	126.1	0.002
ANNELIDA	726.2	166.9	432.3	108.3	0.072	719.8	115.9	481.6	112.1	0.001
Polychaeta	638.7	151.6	368.2	101.9	0.090	643.4	107.1	454.8	107.0	0.001
<i>Streblospio benedictii</i>										
Webster, 1879	304.5	84.1	234.4	87.9	0.413	216.6	80.3	206.4	81.5	0.744
<i>Polydora ligni</i>										
Webster, 1879	142.7	108.3	5.1	5.1	0.216	127.4	42.0	30.6	19.1	0.019
<i>Capitella capitata</i>										
(Fabricius, 1780)	54.8	19.1	40.8	10.2	0.400	98.1	33.1	72.6	25.5	0.135
<i>Neanthes succinea</i>										
(Frey & Leuckart, 1847)	63.7	20.4	12.7	5.1	0.007	87.9	26.8	35.7	12.7	0.016
Nereidae, unidentified	61.2	11.5	51.0	8.9	0.513	26.8	14.0	31.8	12.7	0.545
<i>Mediomastus californiensis</i>										
Hartman, 1944	3.8	2.6	16.6	7.6	0.108	31.9	14.1	20.4	8.8	0.182
<i>Heteromastus filiformis</i>										
(Claparede, 1864)	8.9	3.8	8.0	5.1	0.763	28.0	14.0	14.0	6.4	0.124
<i>Tharynx marione</i>										
(Saint-Joseph, 1894)	0.0	0.0	2.6	2.6	0.326	7.3	3.8	39.5	24.2	0.146
<i>Parandalia ocularis</i>										
Emerson & Fauchald, 1971	14.0	6.6	15.3	6.9		3.8	2.2	2.6	1.2	
<i>Hobsonia gunneri</i>										
(Hartman, 1951)	1.3	0.8	0.0	0.0		7.6	2.2	3.8	1.4	
<i>Eteone heteropoda</i>										
Hartman, 1951	2.6	1.3	0.0	0.0		3.8	1.5	2.6	1.3	
<i>Paraonis fulgens</i>										
(Levinsen, 1884)	7.6	6.9	2.6	2.2		0.0	0.0	0.0	0.0	
<i>Polydora caulleryi</i>										
Mesnil, 1897	2.2	2.2	6.4	6.4		0.0	0.0	0.0	0.0	
<i>Polydora cf. socialis</i>										
(Schmarda, 1861)	0.0	0.0	2.6	2.2		0.0	0.0	0.0	0.0	
<i>Paraprionospio pinnata</i>										
(Ehlers, 1901)	1.3	1.3	0.0	0.0		0.0	0.0	0.0	0.0	
<i>Leptoscoloplos fragilis</i>										
(Verrill, 1873)	0.0	0.0	1.3	1.3		0.0	0.0	0.0	0.0	
<i>Diopatra cuprea</i>										
(Bosc, 1802)	1.3	0.6	0.0	0.0		0.0	0.0	0.0	0.0	
Oligochaeta	87.9	43.3	63.7	44.6	0.691	76.4	25.5	25.5	10.2	0.017

Table 2. Continued.

Taxon	Fall 1990				Spring 1991			
	Interculm		Interplant		Interculm		Interplant	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
CRUSTACEA								
Calanoida (unident. spp.)	17.8	12.1	12.7	8.8	7.6	3.2	3.8	2.8
Cyclopoida (unident. spp.)	1.3	0.8	3.8	1.9	0.0	0.0	0.0	0.0
Harpacticoida (unident. spp.)	2.6	1.5	0.0	0.0	0.0	0.0	0.0	0.0
Curripedia								
<i>Balanus</i> (unident. spp.)	12.7	6.3	5.1	3.6	3.8	3.8	1.3	0.6
Peracarida	415.3	183.5	58.6	38.2	172	40.8	35.7	14
Tanaidacea								
<i>Hargeria rapax</i>								
(Harger, 1879)	80.3	31.9	37.3	28	35.7	10.2	22.9	12.7
Mysidacea (unident. sp.)	1.3	0.8	1.3	0.8				0.270
Cumacea (unident. sp.)	1.3	0.9	0.0	0.0				
Isopoda (unident. sp.)	14.0	5.5	5.1	2.9	11.5	3.6	2.6	1.4
Amphipoda	318.1	159.3	15.3	8.9	124.9	34.4	9.7	3.8
<i>Corophium louisianum</i>								0.001
Shoemaker, 1934	2.6	2.2	0.0	0.0				
<i>Corophium</i> spp.	290.9	158	6.8	3.8	45.0	16.6	1.8	1.3
<i>Gammarus mucronatus</i>								0.014
Say, 1818	24.2	10.2	6.4	3.8	70.1	24.2	5.7	3.8
<i>Ampelisca abdita</i>								0.011
Mills, 1964	0.0	0.0	0.0	0.0	5.1	3.3	2.6	1.8
<i>Orchestia</i> cf. <i>grillus</i>								
Bosc, 1802	0.0	0.0	1.3	1.3	3.8	2.7	0.0	0.0
<i>Orchestia</i> spp.					1.3	0.6	0.0	0.0
Hyperidae sp.	0.0	0.0	1.3	1.3	0.0	0.0	0.0	0.0
Decapoda								
<i>Palaeomonetes pugio</i>								
Holthius, 1949	1.3	0.9	1.3	0.8	0.0	0.0	0.0	0.0
Xanthidae sp.	5.1	3.4	0.0	0.0	2.6	1.3	0.0	0.0
<i>Callinectes sapidus</i>	1.3	0.8	0.0	0.0	0.0	0.0	0.0	0.0

to those reported by Rader (1984), especially at his low-elevation *S. alterniflora* marsh locations. Although densities of the abundant polychaete *Neanthes succinea* (Frey & Leuckart, 1847) in his study were not different between his samples with culms and without culms, there were significantly greater densities of this species in the interculm microhabitat during both seasons in the present study (Table 2).

Apparent distribution patterns of organisms in relation to salt marsh plants can be affected by sampling techniques in a variety of ways. For the present study, samples of microalgal pigments and meiofauna were collected with a 2.2-cm-diameter core and included only sediment from the interculm and interplant microhabitats. These samples differed from those used to collect macrofauna because the larger (10-cm-diameter) macrofauna core samples included interculm sediments, sediments from the periphery of the culm clusters, and *S. alterniflora* stems. Animals associated with plant stems, such as amphipods (Van Dolah 1978, Covi and Kneib 1995), may have had elevated densities in these samples even if the organisms were not more abundant in the interculm sediments themselves. In addition, all interplant samples were collected among clusters but as far from culms as possible. If differences exist between the interculm and interplant sediments, a gradient may be present between these microhabitats. Thus, the location of interplant samples in the area between culm clusters may affect results. Bell *et al.* (1978) randomly selected interplant sample locations in the space between culm clusters and found few differences in meiofaunal densities between samples with and without culms. In contrast, Rader (1984) collected "bare sediment" (interplant) cores (3.5-cm-diameter) in culm-free areas at least 10 cm in diameter to reduce potential effects of surrounding culms and found significant macrofauna density differences between near culm and bare sediment samples. Similarly, core diameter will affect results; as the diameter of a core sample increases, the ability to distinguish between interplant and interculm microhabitats will decrease. The distribution patterns observed in the present study may also have been affected by the sampling depth of the sediment. In all cores, the upper 5 cm of sediment was sampled, and both meiofauna (Bell *et al.* 1978, Sikora and Sikora 1982) and macrofauna (Goldberg 1996) distributions are vertically stratified in marsh sediments. However, Bell *et al.* (1978) did not observe any interaction between the vertical distribution of meiofauna and interculm/interplant distributions.

Differential settlement, reproduction, growth, and survival could all account for differences in populations of meiofauna and macrofauna in these two microhabitats. Passive settlement processes seem impor-

tant in determining small-scale distributions of meiofauna in relation to the microtopography of the marsh surface (Fleeger *et al.* 1995), and reductions in water flow associated with plant stems may result in increased densities in interculm sediments (Fonseca *et al.* 1982, Eckman 1983). Fleeger *et al.* (1995) found that in moving water, passive settlement is apparently more important in determining small-scale meiofauna distributions; when tidal fluctuations and flow are limited, active dispersal processes may be favored. However, water currents can also resuspend sediments and meiofauna, and the effects of flow intensity on meiofaunal populations are complex (Fleeger *et al.* 1984). Although tidal flow in Galveston Bay marshes is low in comparison with marshes on other coasts, many of the marshes included in the present study were exposed to substantial wave-generated flows (Delaney *et al.* 2000). Some such flows may have been of sufficient magnitude to resuspend benthic macroalgae and meiofauna.

The wide range of foraging modes and types of food eaten by meiofauna and macrofauna make it difficult to generalize regarding any potential effects of *Spartina alterniflora* stems on foraging relationships. Positive relationships between animal abundance and sediment macroorganic matter, including sediment roots and rhizomes, (Osenga and Coull 1983, Rader 1984), may reflect increased foraging opportunities for sediment deposit feeders. Although no difference in microalgae biomass between the interculm and interplant sediments was found, algal production may differ between the microhabitats. Increased densities of herbivores in the interculm microhabitat may also be exploiting microalgae on *S. alterniflora* stems. Sullivan and Moncreiff (1990) found the food web in a Mississippi salt marsh to be based primarily on algal-derived carbon rather than carbon derived from vascular plants. Particulate organic matter and resuspended benthic microalgae resettling from the water column may also provide food for surface deposit and suspension feeders, and the same physical processes that affect passive settlement of larvae may enhance this food resource near *S. alterniflora* stems.

Survival of meiofauna and macrofauna may be relatively high in the interculm microhabitat. The physical exclusion of nekton and large benthic predators from the clusters of smooth cordgrass culms and the structural complexity provided by above-ground stems and below-ground roots and rhizomes should decrease predator-related mortality (Vince *et al.* 1976, Van Dolah 1978, Nelson 1979, Marinelli and Coull 1987). Bell (1980) found that meiofaunal populations increased when motile macroepifauna were experimentally excluded from the marsh surface by cages, although this effect varies (Fleeger *et al.* 1981). Both



laboratory and field experiments have shown that meiofaunal and macrofaunal populations are susceptible to rapid depletion by predatory decapod crustaceans (Bell and Coull 1978, Gregg and Fleeger 1998, McTigue and Zimmerman 1998) and small fishes (Fitzhugh and Fleeger 1985, McCall and Fleeger 1993, Gregg and Fleeger 1997). Survival of organisms in interculm sediments might also be enhanced by increased oxygen levels associated with living root material (Teal and Kanwisher 1966, Osenga and Coull 1983).

The present results indicate that some significant differences occur in densities of meiofauna and macrofauna between interculm and interplant salt marsh microhabitats. Thus, the small-scale spatial distribution of these organisms on the marsh surface appears related to the proximity of *S. alterniflora* culms. Interculm sediments comprise from less than 10% in some marshes to over 30% of the salt marsh surface in others, and these small-scale distribution patterns need to be considered when designing sampling programs in salt marshes. Further research is needed to determine exactly what factors are primarily responsible for the differences in population density between these two microhabitats. The relative importance of such factors as shelter from predation, from water dynamics, from desiccation at low tide, differences in intensity of solar irradiation, rate of trapping of suspended particles, and alteration of surface sediment texture by emergent root material, among others should be considered in this regard.

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